

The effects of surface geology and stream size on freshwater mussel (*Bivalvia*, Unionidae) distribution in southeastern Michigan, U.S.A.

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SUMMARY. 1. Stream size and surface geology are the two major environmental features that control the distributions of the thirty-four species of unionid mussels living in the streams of southeastern Michigan.

2. Surface geology, a previously unrecognized factor in the ecology of freshwater mussels, acts to regulate the hydrology, slope and turbidity of streams in the study area.

3. Reciprocal averaging ordinations are used to aid the description of the habitats occupied by each mussel species.

Introduction

It has long been known that mussel faunas change predictably along the length of a stream, shifting in composition from species characteristically found in small brooks to those that live in the largest rivers (e.g. Ortmann, 1919; Baker, 1926; and especially van der Schalie, 1938). However, intensive study of any local fauna (one having no intersite variation due to zoogeographic history) will reveal distributional patterns that are not strictly related to stream size: a species will be abundant in some streams of a given size, but absent from others. The presence of such distributional anomalies might be accepted as an inevitable consequence of working with samples drawn from a complex natural world subject to the action of numerous variables. They might, however, indicate that environmental features other than stream size are important in determining the distribution of mussel species.

During surveys of the unionid mussels of some Michigan streams, it soon became apparent that the lack of fit of faunal composition to stream size was related to the complex glacial geology of southern Michigan. Streams flowing

over different glacial formations have different characteristics and support different mussel faunas. These assertions are documented in this paper, and the habitats of the various mussel species in southeastern Michigan are defined.

The study area

Southeastern Michigan is drained by four major river systems: the Clinton, Rouge, Huron and Raisin Rivers (Fig. 1). In the north and west edges of the region, outwash plains are punctuated by kettles and kames (basins and mounds, respectively, formed near the edge of a stagnant glacier). These deposits, which will be referred to as 'outwash', are composed mainly of sand and gravel. Soils here have high infiltration capacities. As a result, there is little surface runoff, and the streams maintain steady flows throughout the year (Fig. 2). Stream gradients on the outwash plains are very low (Fig. 3), and the stream courses are interrupted by marshes and lakes. Because of the presence of these lakes, which act as settling basins, and because of the small contribution of surface runoff, the streams are usually clear, and the fluctuations in temperature, water chemistry, current speed, etc., are presumably relatively small.

South and east of the outwash plains lies a band of rolling end moraines and till plains.

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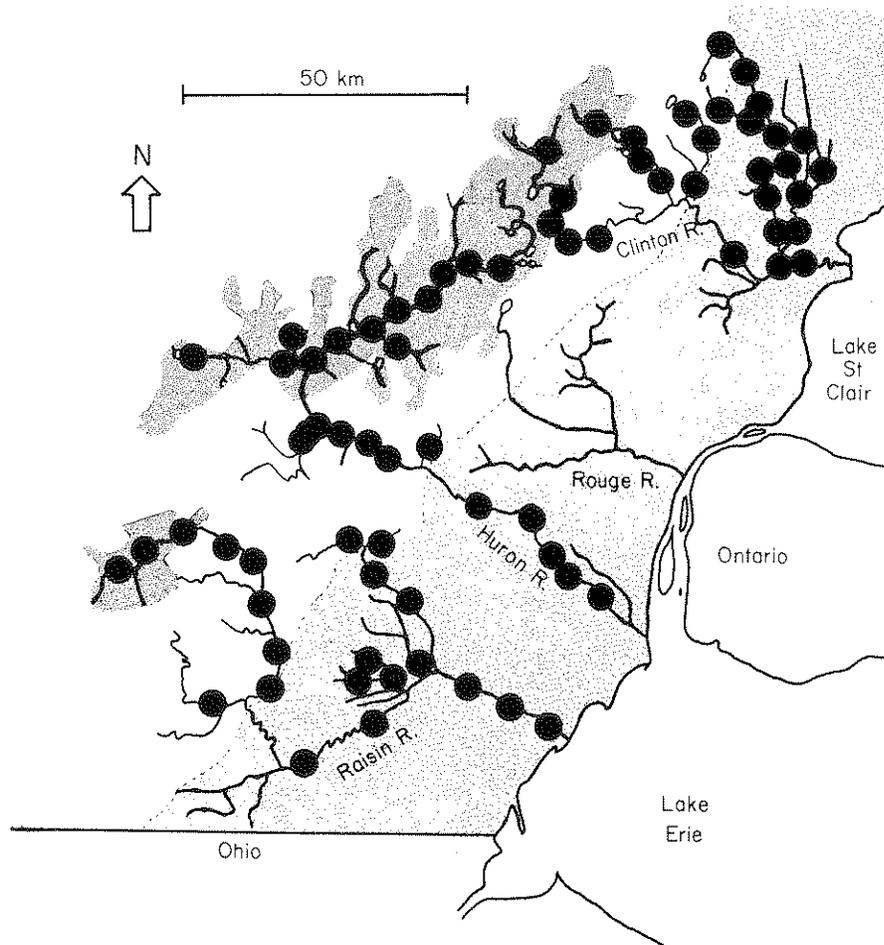


FIG. 1. The study area in southeastern Michigan. The major surface formations are outwash plains (dark stippling), end moraines and till plains (white), and lake plains (light stippling). Each study segment is marked by a dot. See text for further description. Modified from Martin (1955).

Although this band contains some gravelly kames, especially to the north, deposits here are mostly compact and clayey. These deposits will be termed 'moraines'. Streams running on moraines also have relatively little variability in discharge (Fig. 2), but are somewhat more variable than those on outwash. Lakes are rare and stream gradients are high (Fig. 3).

High level proglacial lakes inundated the area to the east of the end moraines, leaving very flat 'lake plains' of clay and some sand. Soils of the lake plain have low infiltration capacities, so the streams there are prone to flooding and drying down (Fig. 2). For example, Coon Creek (a lake plain stream) carries $50-75 \text{ m}^3 \text{ s}^{-1}$ of water during spring floods, but

is reduced by late summer to a series of unconnected stagnant pools. Because the soils are clayey, and because most of the land on the lake plain is farmed, streams are often turbid, even during periods of low flow. There are no natural lakes on the lake plain, and stream gradients are low (Fig. 3).

Drift of pre-Wisconsin age underlies all of these deposits, but its nature is poorly known. Total drift thickness varies from about 15 m on the southeastern parts of the lake plain to more than 100 m in the upper Huron and Clinton River drainages in the northwest. Further information on the geology of the region is available in Leverett & Taylor (1915), Martin (1955), Nowlin (1973), Knutilla & Allen (1975)

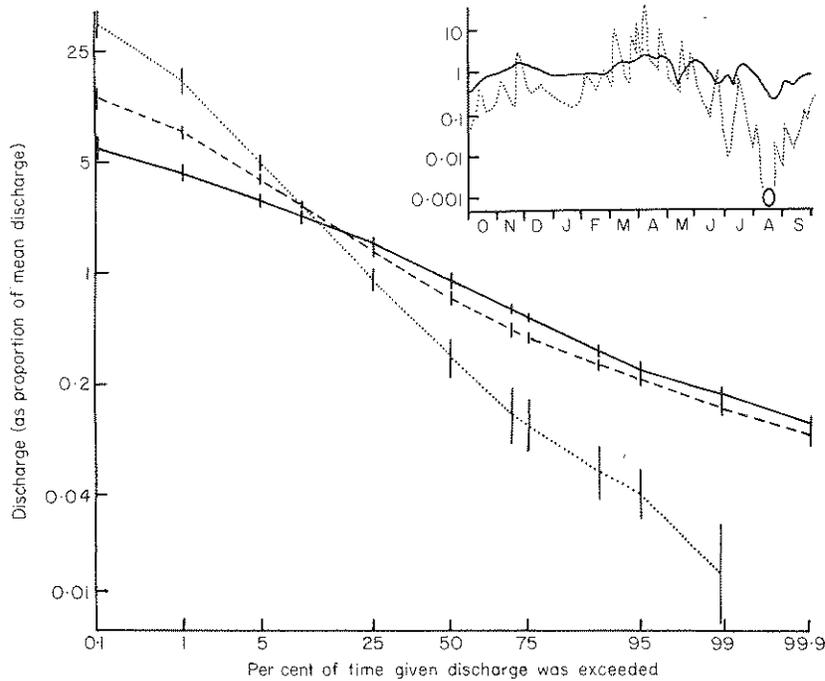


FIG. 2. Hydrologic variability in the streams of southeastern Michigan. The inset shows the hydrographs of the upper Clinton River (solid line), which drains outwash, and Coon Creek (dotted line), which drains lake plain. The ordinate for the inset is the same as the ordinate for the main figure. The main figure shows flow-duration curves for streams draining each of the major formations: outwash (solid line), moraines (dashed line) and lake plain (dotted line). Steeper curves indicate greater variability of flow. The curves are means of several stations; vertical bars show ± 1 SE. All data from the United States Geological Survey.

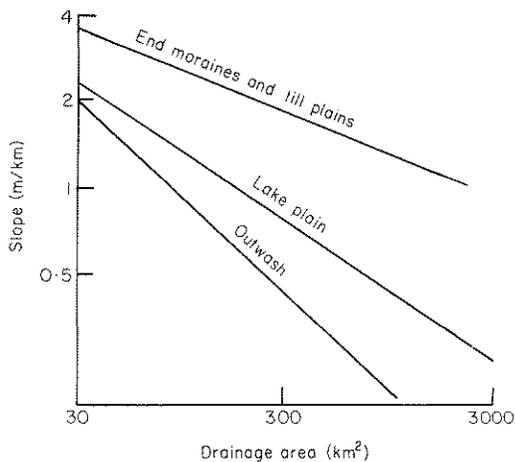


FIG. 3. Slopes of streams running on different surface formations in southeastern Michigan. Lines are fitted by linear regression through data taken from Nowlin (1973), Knutilla & Allen (1975) and Larson *et al.* (1975). Note that both axes have logarithmic scales.

and Larson, Allen & Hanson (1975), from which the above account was summarized. Although southeastern Michigan was originally covered by mixed deciduous forests, it is now occupied primarily by row crops, pastures and urban areas.

All streams in the area are fertile, well-buffered, warmwater streams (Table 1). There are some differences in the water chemistry of streams draining the different surface formations, but as Nowlin (1973) has pointed out, the differences are due not to the surface formations themselves, but to the underlying bedrock formations and municipal pollution, which are partly coincident with the surface formations.

Materials and Methods

The mussel faunas of southeastern Michigan are well known, mainly through the work of van der Schalie and his colleagues at the University

TABLE 1. Water chemistry of streams draining different surface formations in southeastern Michigan. Values shown are means \pm one standard deviation for the seventy-four stations sampled by Nowlin (1973) and Knutilla & Allen (1975) during periods of base flow. True annual average values would probably lie somewhat lower than those shown in the table

	Lake Plain	Moraine	Outwash
No. of stations	40	24	10
HCO ₃ ⁻ (mg l ⁻¹)	253 \pm 46	249 \pm 41	239 \pm 31
SO ₄ ²⁻ (mg l ⁻¹)	94 \pm 33	77 \pm 53	37 \pm 14
Cl ⁻ (mg l ⁻¹)	50 \pm 35	18 \pm 9	21 \pm 18
pH	8.2 \pm 0.3	8.2 \pm 0.2	8.1 \pm 0.2
Conductivity (μ S cm ⁻¹ (20°C))	703 \pm 194	598 \pm 107	491 \pm 56

of Michigan Museum of Zoology (UMMZ). This work has been supplemented with my own surveys. The locality records for mussels were taken from van der Schalie (1938, Table 4), Strayer (1979, 1980), and unpublished records of the UMMZ. Because the available records are semiquantitative at best, only presence/absence data were used.

For convenience, the streams were divided into 8.1 km (5 mile) segments using the stream mileages given in Nowlin (1973), Knutilla & Allen (1975) and Larson *et al.* (1975), and collection records were combined within each segment. Segments for which no (or incomplete) collections were available were discarded. The Rouge River was excluded from the study because van der Schalie (1938, p. 14) has presented evidence that it has had a different zoogeographic history from the other streams in the area. The seventy-five segments remaining formed the basis for the present study (Fig. 1).

Physical data for the streams and their catchments were taken from Nowlin (1973), Knutilla & Allen (1975) and Larson *et al.* (1975). Drainage area was used as a measure of stream size. Mean annual discharge (MAD, l s⁻¹) can be estimated from drainage area (DA, km²) by:

$$\text{MAD} = 2.54 \times \text{DA}^{1.15} \quad (1)$$

This relationship was derived by fitting a power law through data from the thirty-three gauging stations in the study area (Strahler, 1964).

Several of the mathematical ordination techniques available in Cornell's ORDIFLEX package (Gauch, 1977) were used to develop descriptions of faunal patterns. As others have reported (e.g. Gauch, Whittaker & Wentworth, 1977; Culp & Davies, 1980), reciprocal averaging (Hill, 1973) gave the most interpretable results and will be used below. In reciprocal averaging (RA), the computer is given a list of the species present at each of the sampling sites. It uses this information to construct a primary axis of faunal variation; that is, sites are ordered so that those having the least similar faunas form the endpoints of the axis, and those having similar faunas lie near to one another on the axis. Then the remaining variation in the data set is used to construct a second axis of faunal variation that is independent of the first axis. The algorithm can repeat this process to produce many more axes, but only rarely are more than two or three axes useful in representing faunal variation (e.g. Gauch, 1982).

The ordering of sites by RA depends only on the faunas of those sites and uses no environmental data. Thus, the ordination results provide an objective independent measure of variation in faunal composition that can be tested by the investigator against the environmental features suspected to be responsible for that variation.

Species may be of such infrequent occurrence that their distributions cannot be well defined by the ordination algorithm. Inclusion of such species may blur the results of an ordination without adding much useful information (Gauch, 1982, p. 152). Because of this, the seven species that were present in fewer than three stream segments were excluded.

Mussel nomenclature follows Burch (1975).

Results

The primary axis of variation in the mussel faunas is related to stream size (Fig. 4). The papers of van der Schalie (1936, 1938, 1941) contain a great deal of information showing how the mussel species of southern Michigan are distributed according to stream size. Because the headwaters-to-mouth succession proceeds mainly by species addition rather than by species replacement, there is an increase in species richness with stream size (Fig. 5).

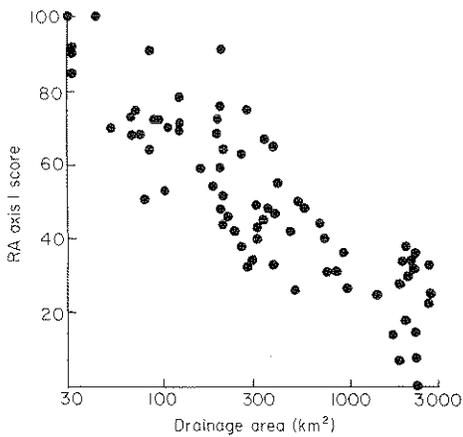


FIG. 4. The relationship of the primary axis of mussel faunal variation to stream size. Each point represents a study segment plotted according to its drainage area (note the logarithmic scale) and the composition of its mussel fauna (as its score on RA axis 1). $r = -0.86$, $P < 0.001$.

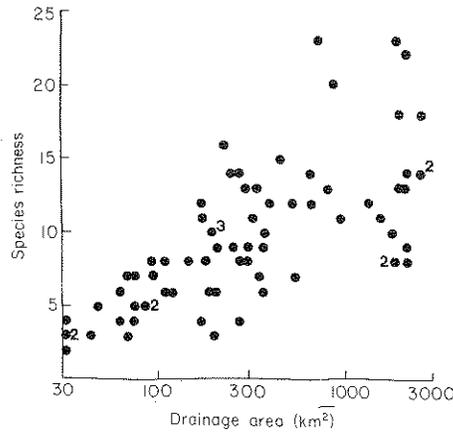


FIG. 5. Mussel species richness as a function of stream size. Numbers indicate the number of observations falling on the same point. $r = 0.68$, $P < 0.001$.

Others have reported a similar increase in species richness for stream mussels (e.g. van der Schalie, 1938) and stream fish (e.g. Kuehne, 1962; Sheldon, 1968; Horwitz, 1978).

The correspondence between stream size and mussel distribution is, however, not perfect. To show this, I have plotted the collection records for two common mussel species by stream size

(Fig. 6, lower panels). If stream size were the sole factor that controlled the distributions of these two species, there would be no mixing of presences (black) and absences (white) in the figure; that is, all streams of the appropriate size would contain the species and all others would not. This is certainly not the case for either species in Fig. 6. While it is possible to recognize that each species inhabits streams in a

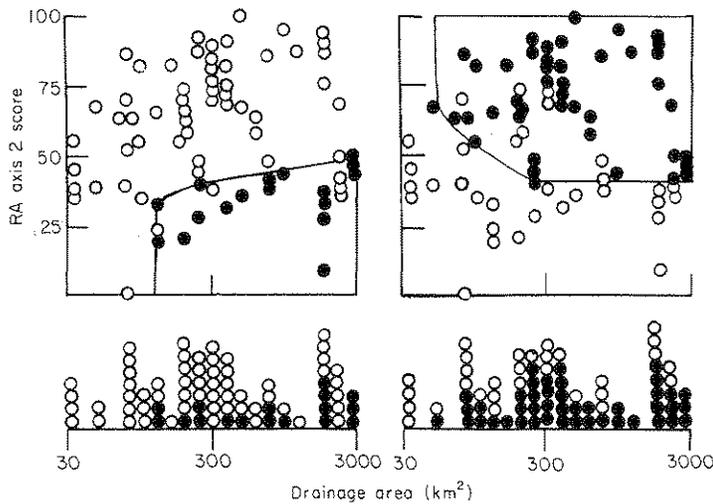


FIG. 6. Lower panels. Distribution of *Amblema plicata* Say (left) and *Elliptio dilatata* Rafinesque (right) as a function of stream size. Each circle represents a study segment of the indicated drainage area and is filled if the species is present there. Upper panels. Distribution of the same two species as a function of stream size and RA axis 2, which represents surface geology (see text). The solid line delimits the approximate ecological range of each species (see text)

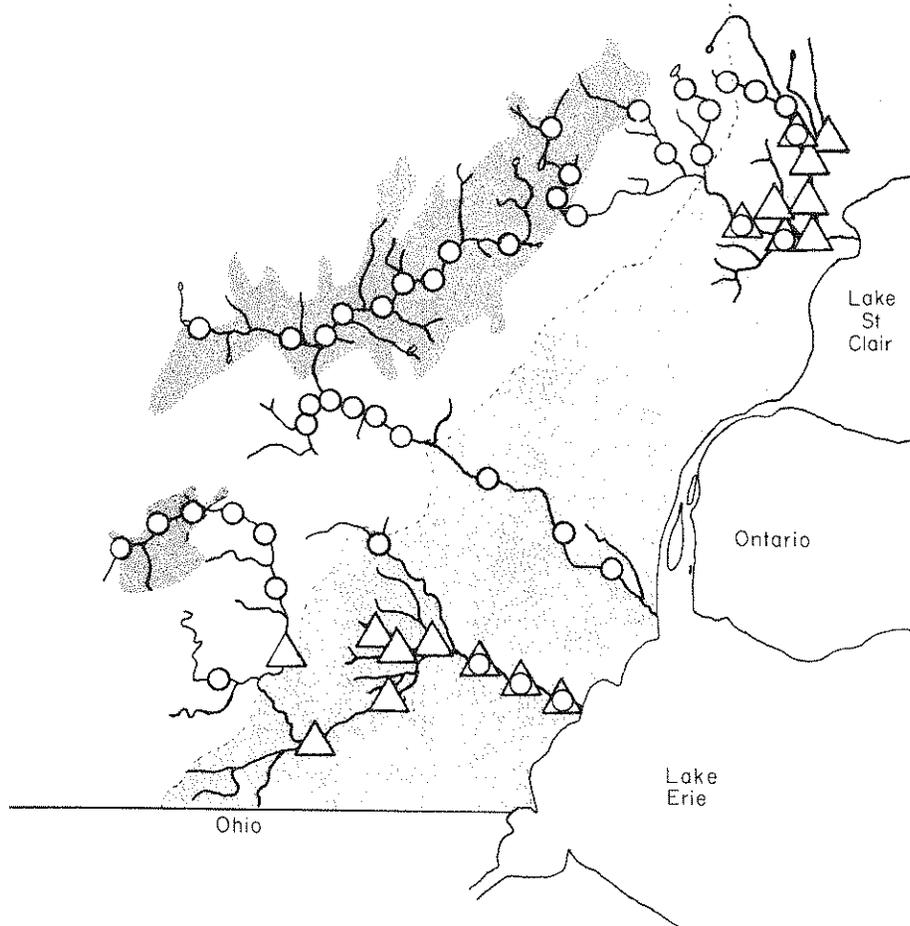


FIG. 7. Distribution of *Amblyma plicata* (triangles) and *Elliptio dilatata* (circles) on a surface geology map of southeastern Michigan. Surface formations as in Fig. 1.

particular size range (120–3000 km² for *Amblyma plicata* and 50–3000 km² for *Elliptio dilatata*), there are many segments within these ranges that lack the species. Stream size alone is obviously not sufficient to define the habitats of the two species.

The reason for this becomes clear when collection records for these two species are superimposed on a map of the surface formations in southeastern Michigan (Fig. 7): the animals are distributed according to surface geology as well as stream size. *Amblyma plicata* is widespread in the lake plain streams (present in sixteen of the twenty-five segments having drainage areas of more than 120 km²), but has been found at only one site on the other

formations. *Elliptio dilatata*, on the other hand, is widespread and abundant in streams on outwash and moraines (present in thirty-three of the forty-one segments draining more than 50 km²), but is much more sparsely represented on the lake plain (present in eleven of the twenty-nine segments that drain more than 50 km²). Furthermore, *E. dilatata* is rarely abundant in streams on the lake plain (van der Schalie, 1938; Strayer, 1980). All of the lake plain streams that do contain *E. dilatata* have large portions (>40%) of their catchments on the other surface formations; these streams are in some respects (e.g. hydrology) intermediate between typical lake plain streams and typical moraine/outwash streams. *E. dilatata* has never

been found in a stream that drains lake plain exclusively. Thus, *E. dilatata* is mainly a creature of streams on outwash and moraines that drain more than 50 km², while *A. plicata* is almost entirely restricted to streams on the lake plain that have drainage areas of more than 120 km².

Further evidence that mussel faunas are influenced by surface geology comes from the ordination results. Because the second RA axis is constrained to be independent of the first axis, the second axis scores are uncorrelated with stream size ($P > 0.50$ against drainage area or log₁₀ drainage area), and can be thought of as expressing variation in faunal composition after the effects of stream size are removed. By examining Table 2, in which the stream segments are classified according to surface geology and second axis scores, it can be seen that surface geology is strongly correlated with the variation in mussel faunas not due to stream size. Streams with low second axis scores (0–50) are on the lake plain, streams with high scores (75–100) are on outwash, and streams with intermediate scores (50–75) are on moraines. There are exceptions to this pattern: for example, seven of the segments with high second axis scores are on moraines, not outwash. However, all seven of these, while running on moraines, have catchments dominated by outwash, not moraines. As was mentioned in the discussion of *E. dilatata*, these streams have affinities to streams running on outwash, and might as easily be classed with the outwash streams as with the moraine streams. Likewise, the two lake plain segments having scores of 50–75 drain considerably more outwash and moraines than they do lake plain. Thus, the second axis scores can be used to classify the segments by surface geology (either at the segment itself or, in a few cases, of its

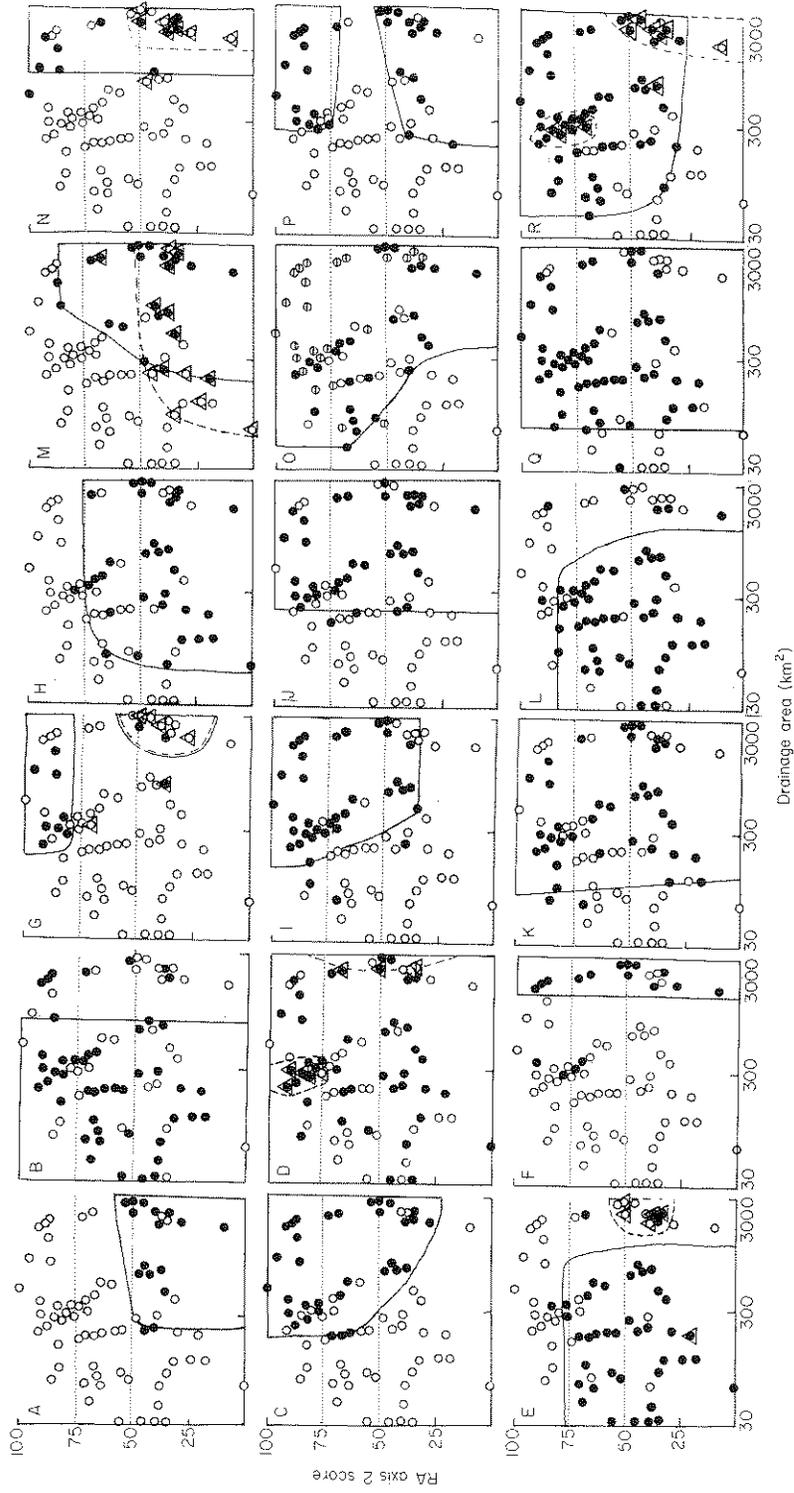
catchment) in the great majority (89%) of cases.

One of the primary goals of this study was to define as clearly as possible the habitats occupied by each mussel species in southeastern Michigan. It would be convenient to plot the distribution of each species along the two major habitat axes simultaneously. Segments can be ordered along the stream size axis by their drainage areas (or mean annual discharges), but it is not clear how to construct a surface geology 'axis'. As indicated in the description of the study area, surface geology has complex effects on several stream properties: hydrology, slope and turbidity, to name a few. It seems likely that the geology at the site and the geology of the catchment are both involved. I tried to construct a surface geology 'axis' by calculating for each segment indices based on, for example, the local slope, hydrologic variability, and the proportion of the catchment covered by each surface formation, but none produced a satisfactory ordering of the sites in relation to surface geology. However, as noted in the previous section, the second RA axis is well correlated with surface geology. As a result, I have used the second RA axis as the best surrogate for a surface geology axis when defining species habitats. The utility of the surrogate axis may be seen in Fig. 6 (upper panels), in which the ecological distributions of *Elliptio dilatata* and *Amblema plicata* are presented. *A. plicata*, which lives in streams on the lake plain (cf. Fig. 7), is found in sites with low second axis scores, while *E. dilatata*, which avoids such streams, is found at sites with high scores. Note that the format adopted in the upper panels of Fig. 6 clearly shows the species response to both habitat axes simultaneously.

Ecological ranges for the other mussel species are shown in Fig. 8. The term 'ecological range' is used here as the habitat analogue of Hutchinson's (1978) realized niche, and may be defined as the portion of habitat space likely to be occupied by a given species. For the purposes of this paper, I have subjectively defined these ranges by drawing a line around the group of sites where a species is frequently present (cf. Hutchinson, 1978, Fig. 104). In some cases (e.g. Figs. 6 and 8A), ecological ranges are sharply defined, while in others (e.g. Fig. 8B, K, L) there is a more gradual change from the part of habitat space where a species is gener-

TABLE 2. Classification of stream segments by surface geology at the site and the second RA axis score

Second RA axis score	Formation		
	Lake Plain	Moraine	Outwash
0–50	29	3	1
50–75	2	18	4
75–100	0	7	11



ally present to the part where it is generally absent, and ranges are imperfectly resolved.

However, examination of higher ordination axes did not yield any interpretable results, and in only two cases are the ranges so poorly resolved as to suggest the existence of other ecological factors. *Pleurobema cordatum* (Fig. 8O) is absent from the entire Huron River system, although conditions there are not apparently different from those in other drainage systems where *P. cordatum* is abundant. Van der Schalie (1938, p. 50) noted, without comment, that *P. cordatum* had not been found in the Huron, and I have no explanation for its absence. The absence of *Lasmigona complanata* from apparently suitable sites in the Raisin River basin (Fig. 8M) may have a zoogeographic basis. It has been suggested that, unlike the other species, *L. complanata* entered the region from the north, by way of the Saginaw-Grand Valley (van der Schalie, 1938, p. 54). If this is true, and reports of range extensions for this species (van der Schalie, 1938; Strayer, 1979) represent its southward spread through the region, then *L. complanata* may be absent from the Raisin basin because it has only recently reached the basin. I expect the species

to spread throughout the lower Raisin drainage in the near future. (Reports of *L. complanata* from the upper Maumee River system (Clark & Wilson, 1912; Strayer, 1979) probably reflect a secondary invasion through the Wabash-Erie Canal, as suggested by Clark & Wilson.)

Discussion

Obviously, mussel distributions are not controlled by stream size and surface geology as such, but rather by some of the many ecological factors associated with them. Many potentially important ecological variables are known or suspected to vary with stream size; e.g. mean current velocity (Ledger, 1981), temperature, mean particle size of the substratum (Leopold, Wolman & Miller, 1964), and the timing and nature of organic inputs (Vannote *et al.*, 1980). However, in the case of unionid mussels (as with most other examples of longitudinal succession in the stream fauna), little is known of the mechanisms by which these environmental changes are translated into faunal distributions.

Surface geology likewise affects a number of the characteristics of streams, but again the

FIG. 8. Distribution of mussel species with respect to stream size and the second RA axis, which is a surrogate for surface geology (see text). The dotted horizontal lines are approximate boundaries between lake plain (0–50), moraines (50–75) and outwash (75–100). Other symbols as in Fig. 6, upper panels. (A) *Actinonaias carinata* (Barnes), a species of larger streams on the lake plain; (B) *Alasmidonta calceolus* (Lea) widespread, but abundant only in small streams; (C) *Alasmidonta marginata* (Say), widespread in medium-sized streams, especially away from the lake plain; rarely abundant; (D) *Anodonta grandis* (Say), of wide ecological range, and *Anodonta imbecilis* (Say) (triangles), from low gradient stretches on outwash and the lake plain, especially where the latter are impounded; (E) *Anodontooides ferussacianus* (Lea), widespread in small streams, but avoiding outwash, and *Carunculina parva* (Barnes) (triangles), from the lake plain in rivers, impoundments, and creeks; (F) *Cyclonaias tuberculata* (Rafinesque), in larger streams everywhere; (G) *Dysnomia triquetra* (Rafinesque), from low gradient stretches on outwash and in the lower courses of rivers, and *Dysnomia torulosa* (Rafinesque) (triangles), scattered in low gradient streams; (H) *Fusconaias flava* (Rafinesque), widespread in medium-sized and small streams, but almost entirely absent on outwash; (I) *Lampsilis fasciola* (Rafinesque), from medium-sized and large streams, very widespread on outwash and less so elsewhere; (J) *Lampsilis ovata ventricosa* (Barnes), found everywhere in moderately large streams; (K) *Lampsilis radiata siliquioidea* (Barnes), very widespread in all but the smallest streams, but not abundant at sites on outwash; (L) *Lasmigona compressa* (Lea), widespread in small streams, but less so on outwash; (M) *Lasmigona costata* (Rafinesque), a species of medium to large streams, especially on the lake plain, and *Lasmigona complanata* (Barnes) (triangles), widespread on the lake plain (although largely absent from the Raisin River drainage), but almost completely missing on other formations; (N) *Ligumia recta* (Lamarck), from larger streams, but rarely abundant, and *Obovaria subrotunda* (Rafinesque), from large streams on the lake plain; (O) *Pleurobema cordatum* (Rafinesque), widespread, especially in medium to large streams away from the lake plain, and inexplicably absent from the Huron River basin (circles with lines); (P) *Ptychobranthus fasciolaris* (Rafinesque), in medium to large streams, but avoiding most of the high gradient moraine streams; (Q) *Strophitus undulatus* (Say), widespread except in a few large and a few small streams; (R) *Villosa iris* (Lea), widespread away from the lake plain and more abundant in small streams, and *Villosa fabalis* (Lea) (triangles), scattered in the lower courses of rivers and in medium-sized streams on outwash. Other species are either invaders from the Great Lakes and restricted to river mouths (*Ligumia nasuta* (Say), *Obliquaria reflexa* (Rafinesque), *Proptera alata* (Say), *Quadrula pustulosa* (Lea), *Quadrula quadrula* (Rafinesque), *Truncilla truncata* (Rafinesque)) or are very rare (*Carunculina glans* (Lea), *Simpsoniconcha ambigua* (Say)).

mechanisms through which the mussel fauna is affected can only be hinted at. Probably the most important feature influenced by surface geology is hydrology: streams draining different surface formations show great differences in patterns of discharge (Fig. 2). Variation in discharge reflects the frequency of floods and droughts, both of which have marked effects on the stream biota (Hynes, 1970). During the periods of extremely low discharge experienced by streams on the lake plain, many mussels are killed by desiccation, heat, or mammalian predation (Strayer, unpublished). In addition, discharge affects current velocity, stream temperatures, water chemistry, and the transport of the organic particles that serve as food for the mussels. For these reasons, hydrologic variability might be important in determining the distributions of mussels and other stream animals.

Horwitz (1978) has recently shown that hydrologic variability is important in determining the structure of fish communities in the American Midwest, and it is likely that this factor is generally important in determining the structure of biotic communities in streams. It would be useful if quantitative measures of hydrologic variability were presented in more papers on stream biology, in cases where such data are available (the United States Geological Survey supplies daily discharge data for many streams in the United States).

There are considerable differences in slope among the streams of different surface formations (Fig. 3). Slope is related to current velocity and particle size of the substratum, both of which have been shown to affect the distribution of stream invertebrates. Species ranges are not well defined with respect to slope alone (note in Fig. 8 that many species are found in both the high gradient moraine streams and in the low gradient outwash streams, for example), so the influence of slope is probably secondary to that of other factors.

Surface geology commonly affects the chemistry of surface waters and by doing so affects biotic distributions (e.g. Clarke & Berg, 1959; Young, 1973; Hutchinson, 1975, pp. 369–390). Although the streams of different surface formations differ in details of water chemistry (Table 1), it is not likely that these differences are important to the mussel fauna. Work on the chemical ecology of the Unionidae has been

concentrated on the roles of low alkalinity (or, equivalently, low concentrations of calcium) or high salinity in restricting mussel distributions (Clarke & Berg, 1959; Cvancara, 1970, 1975; Imlay, 1973). All of the streams in southeastern Michigan have high alkalinities and low salinities in comparison to reported limiting values. Differences in turbidity, though, may be of some importance. High turbidity is thought to be harmful to many mussel species (Ellis, 1936; Fuller, 1974), and many of the streams on the lake plain are very turbid.

Because larval unionids are parasitic on fish (Coker *et al.*, 1921; Pennak, 1978), it is possible that mussels themselves are indifferent to stream size and surface geology, but have distributions determined by those of their hosts. Indeed, fish distributions in southeastern Michigan are related to stream size and surface geology (Smith, Taylor & Grimshaw, 1981). However, the following example shows that more than fish distribution is involved in determining the range of a mussel species.

The hosts of *Amblema plicata* are *Perca flavescens* (Mitchill) and four species of centrarchids (Stein, 1968). These fish are widespread in the study area, and are especially abundant on outwash (Smith *et al.*, 1981; UMMZ records). *A. plicata* is restricted almost entirely to the lake plain, a range much smaller than that of its presumed hosts. This implies that the mussel itself is affected by surface geology. Too little is known of the fish hosts of most other mussel species to perform a similar analysis for them.

The direct application of these results is obviously limited in unglaciated regions and in regions having glacial deposits different from those in southeastern Michigan. However, in many parts of North America there are surface formations and streams similar to those discussed in this paper and there, streams often contain mussel faunas similar to those described for southeastern Michigan. For example, streams of the Red River of the North basin drain a clayey plain in Minnesota and North Dakota, and like the streams of the lake plain in southeastern Michigan, they have high turbidities, low slopes and very variable hydrologies (Cvancara, 1970). Twelve of the thirteen species of mussels found in the Red River drainage (Cvancara, 1970) are lake plain species in Michigan.

Even where surface formations are different

from those in Michigan, mussel species may be found in habitats similar to those described here. For instance, *Elliptio dilatata* appears to avoid muddy low gradient streams, both in Michigan and elsewhere, while *Amblema plicata* is a characteristic species of such habitats. It is not possible to make more definite comparisons with other regions, since malacologists have rarely reported detailed environmental data. It will be interesting to see how well the habitat preferences reported in this paper hold in other areas.

This study clearly shows that the catchment of a stream is partially responsible for the biota of that stream. The distributional patterns discussed in this paper have both components independent of the catchment (Figs 2–5 and 8) and components that depend on the catchment (Figs 2, 3 and 6). In general, conditions at any site along a stream are defined both by constraints that are imposed on all running waters: e.g. hydraulic geometry (Leopold *et al.*, 1964) and by the catchment of that particular stream (Hynes, 1975). By analogy to Margalef (1960), we might call these 'extraregional' and 'regional' effects, respectively. Both are important in determining the nature of a stream, and both must be considered in order to understand the distributions of stream organisms.

Acknowledgments

I am grateful to Dave Mitchell, Sally Valdés-Cogliano, Clyde Asbury, Laura Huenneke, Peter Marks, Bobbi Peckarsky and Frank Vertucci for their thoughtful comments on earlier drafts of this paper. I would also like to thank Bob Hanley and Drs Alex Tompa and J. B. Burch of the UMMZ for allowing me to use the collections under their charge. The United States Geological Survey in Okemos, Michigan, kindly provided the flow-duration data used in the construction of Fig. 2. Financial support for this work was provided by a National Science Foundation Predoctoral Fellowship and from class funds of Biological Sciences 767.

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(Manuscript accepted 6 October 1982)